MEIOTIC STUDIES OF CROSSES BETWEEN FRAGARIA OVALIS AND × F. ANANASSA[1]

By LeRoy Powers

Formerly *senior geneticist,*[2] *Division of Fruit and Vegetable Crops and Diseases Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultura Research Administration, United States Department of Agriculture*

INTRODUCTION

The value of the native Rocky Mountain strawberry (*Fragaria ovalis* (Lehm.) Rydb.) for hybridizing with cultivated varieties (× *F. ananassa* Duch.) to develop new varieties having greater winter hardiness has long been recognized (*2, 8, 10*).[3] However, the karyological investigations of Longley (*17*), East (*4, 5*), Mangelsdorf and East (*18*), Kihara (*13*), Yarnell (*29, 30*), Ichijima (*11*), Fedorova (*6*), Lilienfeld (*15, 16*), Kuz'min (*14*), Rozanova (*25*), and Dogadkina (*3*) show the importance of meiotic studies as an aid to any breeding program involving wide crosses between polyploid species and forms within the genus *Fragaria*. The researches of these investigators emphasize particularly the part that asynapsis, conjugation of more than two chromosomes to form multivalents during meiosis, and type of chromosome conjugation (autosyndesis, allosyndesis, or a combination of the two) may play in the breeding of improved varieties.

The importance of asynapsis and of the conjugation of more than two chromosomes to form multivalents during meiosis lies in the effect that they have upon fruitfulness. By adversely affecting fruitfulness asynapsis of the chromosomes during meiosis, if of frequent occurrence, may be one of the major factors contributing to the failure of a breeding program. Likewise, if homology exists between different genoms coming from the same polyploid species, as well as between genoms coming from different polyploid species, conjugation of more than two chromosomes to form multivalents might be of frequent occurrence. If such were the case, one would expect fruitfulness to be reduced materially, possibly to the extent that the accomplishment of the objectives of the breeding program would be threatened.

Turning to the type of conjugation of the chromosomes, if autosyndesis (the pairing, in a polyploid, of chromosomes derived from the same parent) was occurring, then variation in the F_2 population would be limited largely to that taking place within the F_1 hybrid, and the chances for recombining any of the desirable characters of both parents into a single segregate would be decidedly reduced. On the other hand, allosyndesis (pairing in a polyploid of chromosomes derived from opposite parents) would allow for the maximum segregation of the genes differentiating the interspecific characters. A combination of autosyndesis and allosyndesis would result in an

[1] Received for publication May 11, 1943.
[2] Now principal geneticist, Special Guayule Research Project, U. S. Department of Agriculture.
[3] Italic numbers in parentheses refer to Literature Cited, p. 447.

intermediate condition as regards the possibilities for maximum segregation of these same genes. Consequently, information concerning the type of conjugation of the chromosomes during meiosis of the F_1 hybrids would be of considerable value in planning and conducting a breeding program.

The objectives of the studies herein reported were (1) to determine whether asynapsis and the association of more than two chromosomes to form multivalents during meiosis occur frequently enough to affect a breeding program adversely and (2) to ascertain the type of conjugation that occurs during meiosis of the F_1 plants.

REVIEW OF LITERATURE

With the exception of a few varieties produced by Georgeson (*8*), the cultivated strawberries have descended from crosses involving *Fragaria virginiana* and *F. chiloensis*, both of which are octoploids. The basic number of chromosomes in *Fragaria* is seven; hence, the chromosomes of the cultivated strawberry are comprised of four genoms each having seven pairs of chromosomes. The best available information as to the relation between these four sets of chromosomes and between the chromosomes of different species is that obtained from the genetic and karyological investigations of crosses between species of different chromosome numbers and, to a more limited extent, between species of the same chromosome number.

The investigations of Longley (*17*), East (*4, 5*), Mangelsdorf and East (*18*), Kihara (*13*), and Yarnell (*29, 30*) showed that at least some chromosomes of the four genoms of seven pairs of chromosomes are homologous. Yarnell (*29, 30*), from cytological and genetic studies, came to the conclusion that the four sets of chromosomes of the octoploid had a common origin and that corresponding chromosomes of each set were originally homologous. After examining microsporocytes from diploid-tetraploid and diploid-octoploid crosses, Yarnell reported not only pairing between chromosomes from both parents but also autosyndesis among the remaining genoms of the tetraploid parent and the remaining sets of the octoploid parent. He found that in many cases the counts at first metaphase indicated complete pairing, involving the nonhomologous chromosomes of the extra genom, and, in addition, he found secondary association taking place between disomes.

The findings of Ichijima (*11*), Fedorova (*6*), Lilienfeld (*15, 16*), Kuz'min (*14*), Rozanova (*25*), and Dogadkina (*3*) in regard to the homologous relations between the chromosomes of the octoploid forms are well summarized by the following statement from Rozanova (*25*):

> . . . it may be deduced that the evolution of species of *Fragaria* has proceeded in the direction of autopolyploidy or close allopolyploidy. From this it follows that the hypothesis as to the origin of cultivated varieties from a cross between *F. virginiana* and *F. chiloensis* needs supplementing to the extent of stating that *F. virginiana* and *F. chiloensis* are also probably autopolyploids or close allopolyploids with homologous genoms.

From the above investigations it is evident that the haploid chromosome complement of the octoploid forms of *Fragaria* may be symbolized as follows:

F. ovalis—Ao_1, Ao_2, Ao_3, Ao_4
F. chiloensis—Ach_1, Ach_2, Ach_3, Ach_4

F. virginiana—Av_1, Av_2, Av_3, Av_4
$\times$ *F. ananassa*—Acv_1, Acv_2, Acv_3, Acv_4

These formulas are closely patterned after those given by Rozanova (*25*). The *A* is used to show that all the chromosomes of one species are homologous with the chromosomes of any other and that a certain amount of homology exists between genoms within a species. *Acv* indicates that the genoms of $\times$ *F. ananassa* through hybridization descended from those of *F. chiloensis* and *F. virginiana*.

From the studies of the various workers cited, it can be seen that there are a number of possibilities as regards chromosome behavior during meiosis in the F_1 hybrids between *Fragaria ovalis* and $\times$ *F. ananassa*. Asynapsis may or may not be of frequent occurrence. Associations of more than two chromosomes to form multivalents may be the rule, or such associations may occur occasionally or only very infrequently. Finally, the four genoms from *F. ovalis* may pair during meiosis with the four genoms from the cultivated varieties (allosyndesis); two genoms from *F. ovalis* may pair with two other genoms from that species and hence two genoms of $\times$ *F. ananassa* with two other genoms of that species (autosyndesis); and both allosyndesis and autosyndesis may occur either at random or in disproportionate frequencies.

EXPERIMENTAL MATERIAL AND DESIGN

The parents and F_1 hybrids were used in the studies. The design of the experiment was that of a randomized complete block and the variates were as follows:

Group I (collections of *Fragaria ovalis*): A, 37501; B, 361477; C, 36979.
Group II (F_1 hybrids): A, Dorsett $\times$ 37501; B, Gem $\times$ 361477; C, Fairfax $\times$ 36979.
Group III (varieties of $\times$ *F. ananassa*): A, Dorsett; B, Gem; C, Fairfax.

Each group hereafter will be called a species containing three variates. Although group II cannot strictly be classed as a species, it is clear that any differences between this group and either of the other groups must be due to genetic differences between groups I and III. Hence, from genetic considerations one is justified in considering the genetic variation between these three groups as due to inherent differences between species. It follows that, if the differences between the totals of these three groups can be attributed to chance deviations, it cannot be concluded, so far as these collections and varieties are concerned, that there are any differences between species.

The grouping on the basis of A, B, and C is as follows:

Group A: I, *Fragaria ovalis* (37501); II, F_1 (Dorsett $\times$ 37501); III, $\times$ *F. ananassa* (Dorsett).
Group B: I, *F. ovalis* (361477); II, F_1 (Gem $\times$ 361477); III, $\times$ *F. ananassa* (Gem).
Group C: I, *F. ovalis* (36979); II, F_1 (Fairfax $\times$ 36979); III, $\times$ *F. ananassa* (Fairfax).

Again, each group, which hereafter will be designated as a strain, contains three variates. The totals for groups A, B, and C will show statistically significant differences only if there are genotypic differences between the variates of group I, group III, or both I and III. Hence, one is justified in attributing any differences between A, B, and C to differences between strains.

The measure of asynapsis used in these studies was (1) the number of pollen mother cells in 100 observations showing some univalent chromosomes during metaphase I, (2) the number of cells in 100 observations showing at least 1 lagging chromosome during early telophase I, (3) the number of cells in 100 observations showing some chromosomes not on either equatorial plane during metaphase II, and (4) the number of cells in 100 observations showing some lagging chromosomes during early telophase II in any member of the potential tetrads. Thus, 4 different phases of meiosis were studied. In addition, the previously mentioned 100 pollen mother cells in metaphase I were examined to obtain some estimate of the frequency of occurrence of associations of more than 2 chromosomes during meiosis. Four plants of each variate were included in the studies, and 25 cells of each plant were examined. The 4 plants were from 4 different replicates.

With the present limited knowledge of the morphology of the strawberry chromosomes, it is not possible to determine through cytological examination of the stages of division whether autosyndesis, allosyndesis, or a combination of the two is occurring during meiosis. However, indirect but reliable evidence as to the type of conjugation that is occurring can be obtained by studying the means of certain characters of the parents and the hybrid populations.

The young anthers were killed in a solution of 3 parts of absolute alcohol to 1 part of glacial acetic acid and stored in 70-percent alcohol. Belling's (*1*) iron-acetocarmine method was employed in staining the material.

At this time it should be noted that the plants of any particular collection may not be alike genetically. For example, collection 37501 is composed of at least two strains, one of which has pistillate flowers while the other has perfect flowers. The strain possessing the perfect flowers was used in the cytological studies.

ANALYSIS OF THE DATA

Since the data were enumeration data, the method of analysis chosen was to partition χ^2 into its components (see Fisher, *7*) and calculate the heterogeneity χ^2 when it seemed desirable. However, the formulas developed and used in calculating the different χ^2's are not available elsewhere. Therefore, since they are of general application (particularly for enumeration data such as those obtained in germination studies), and since they materially simplify the calculations, detailed illustrations of their application are given.

The components of χ^2 together with their corresponding degrees of freedom are as follows:

Variation due to:	*Degrees of freedom*
Main effects	7
Species	2
Strains	2
Phases	3
Interactions	28
Species × strains	4
Species × phases	6
Strains × phases	6
Species × strains × phases	12
Total	35

The relation between these components and the division used in an analysis of variance is readily recognized.

The formula employed in obtaining χ^2 for the main effects, interactions, and total is as follows:

$$\chi^2=\left[\left(\frac{N}{Sx.Nu}Sx^2\right)-Sx\right]+\frac{Sx}{Sy}\left[\left(\frac{N}{Sx.Nu}Sx^2\right)-Sx\right]$$

in which

$N=$ total number of items classified
$Nu=$ number of items classified for the lowest category of the table
$x=$ number of items in any one category showing one or the other of the alternative phenomena
$y=$ number of items in any one category showing the other alternative phenomenon.

The detailed calculations for obtaining the total χ^2 for the data given in table 1 are given in table 2.

TABLE 1—*Univalent and lagging chromosomes in 100 cells of collections of Fragaria ovalis, varieties of × F. ananassa, and their F_1 hybrids during meiosis*

DETAILED DATA NOT GROUPED

Variate	First division (I)		Second division (II)		Total
	Metaphase	Telophase	Metaphase	Telophase	
Fragaria ovalis:	*Number*	*Number*	*Number*	*Number*	*Number*
37501	4	5	2	4	15
361477	6	4	3	1	14
36979	8	3	3	4	18
Total	18	12	8	9	47
F_1 hybrid:					
Dorsett × 37501	3	0	2	0	5
Gem × 361477	1	2	1	0	4
Fairfax × 36979	5	4	4	5	18
Total	9	6	7	5	27
× *F. ananassa:*					
Dorsett	2	1	0	1	4
Gem	5	2	2	1	10
Fairfax	1	0	3	2	6
Total	8	3	5	4	20

DATA GROUPED FOR SPECIES AND STRAINS

Species group	Row symbol	Sets [1] involving—			
		37501 and Dorsett	361477 and Gem	36979 and Fairfax	Total
Fragaria ovalis	r_1	15	14	18	47
F_1 hybrids	r_2	5	4	18	27
× *F. ananassa*	r_3	4	10	6	20
Total		24	28	42	94

[1] Column symbol for column 3=*a*, for column 4=*b*, and for column 5=*c*.

To complete the illustration of the method of partitioning total χ^2 into its components, the data grouped on the basis of one of the interactions need to be considered (see table 1). The calculations are given in table 2. The χ^2 for the data based on species and strains

is 27.549. But this χ^2 for species and strains is composed of the χ^2 due to differences between species, the χ^2 due to differences between strains, and the χ^2 due to the interaction between species and strains. The χ^2 values for species and strains, also given in table 2, are 12.868 and 5.855. Subtracting these two values from the χ^2 value 27.549 gives the χ^2 (8.826) attributable to the interaction between species and strains.

TABLE 2.—*Details for calculating total and partitioned χ^2's for data in table 1*

Formula	Total χ^2	χ^2 for species and strains	χ^2 for species	χ^2 for strains
N	3,600	3,600	3,600	3,600
Nu	100	400	1,200	1,200
Sx	94	94	94	94
Sy	3,506	3,506	3,506	3,506
Sx^2	376	1,262	3,338	3,124
$Sx.Nu$	9,400	37,600	112,800	112,800
$\frac{N}{Sx.Nu}$	0.382978723	0.095744681	0.031914894	0.031914894
$\frac{N}{Sx.Nu}Sx^2$	144.000000	120.829787	106.531916	99.702129
$\left(\frac{N}{Sx.Nu}Sx^2\right)-Sx$	50.000000	26.829787	12.531916	5.702129
$\frac{Sx}{Sy}$	.026811181	.026811181	.026811181	.026811181
$\frac{Sx}{Sy}\left(\frac{N}{Sx.Nu}Sx^2\right)-Sx$	1.340559	.719338	.335995	.152881
$\left[\left(\frac{N}{Sx.Nu}Sx^2\right)-Sx\right]$				
$+\frac{Sx}{Sy}\left[\left(\frac{N}{Sx.Nu}Sx^2\right)-Sx\right]$	51.340559	27.549125	12.867911	5.855010
χ^2	51.341	27.549	12.868	5.855

Tables similar to the lower part of table 1 can be compiled for species and phases and for strains and phases. The methods of calculating the different χ^2's for the two resulting tables are identical with those used in calculating the various χ^2's for species and strains, and hence need not be given here. The χ^2 for the second-order interaction (species$\times$strains$\times$phases) may be obtained by subtracting the χ^2's for main effects and the χ^2's for the first-order interactions from the total χ^2, which, as previously calculated, is 51.341. All of these χ^2's are listed under Experimental Results (see table 4).

From table 2 and a probability table for χ^2, it can be seen that the odds are rather great against deviations as large as those noted between species occurring by chance. The same, to a lesser extent, is true of the differences between strains. This means that the interaction χ^2 (8.826) is not suitable for testing whether the deviations between the frequency distributions of table 1 for species in respect to strains can be attributed to chance (see Mather, *19*). Hence, it is necessary to calculate a heterogeneity χ^2.

The formula employed in calculating the heterogeneity χ^2 i sas follows:

$$\chi^2 = W + W'$$

in which

$$W = \frac{Sx}{Sa}\left(\frac{a_1^2}{Sr_1}+\frac{a_2^2}{Sr_2}+\ \ldots\ +\frac{a_n^2}{Sr_n}\right)+\frac{Sx}{Sb}\left(\frac{b_1^2}{Sr_1}+\frac{b_2^2}{Sr_2}+\ \ldots\ +\frac{b_n^2}{Sr_n}\right)$$
$$+\ \ldots\ +\frac{Sx}{Sz}\left(\frac{z_1^2}{Sr_1}+\frac{z_2^2}{Sr_2}+\ \ldots\ +\frac{z_n^2}{Sr_n}\right)-Sx$$

W' is obtained by substituting the values of y for those of x in table 1 and solving the formula just given for W. For example, in substituting y for x, cell r_1, a_1 becomes 385 (400−15) instead of 15; r_2, a_2 becomes 395 (400−5); etc. Explanations of other symbols follow:

Sx=total number of the items showing one or the other of the alternative phenomena

Sy=total number of the items showing the alternative phenomenon

$Sa, Sb, \ldots, Sz$=total number of items in the designated column

$a_1, a_2, \ldots, a_n$=number of items in the designated category of column a

$b_1, b_2, \ldots, b_n$=number of items in the designated category of column b

$z_1, z_2, \ldots, z_n$=number of items in the designated category of the last column

$Sr_1, Sr_2, \ldots, Sr_n$=total number of items in the designated row.

From the above formula it will be noted that $a_1^2, b_1^2, \ldots, z_1^2$ are divided by Sr_1. Hence, machine calculation can be much simplified by expressing Sr_1 as a decimal fraction and locking the common multiplier in the machine. The same is true for the other calculations involving Sr. The detailed calculations for the lower part of table 1 follow:

$$Sx=94;\ Sa=24;\ Sb=28;\ Sc=42$$

$$S\left(\frac{a^2}{Sr}\right)=6.513160;\ S\left(\frac{b^2}{Sr}\right)=9.762806;\ S\left(\frac{c^2}{Sr}\right)=20.693617$$

$$\frac{Sx}{Sa}=3.916667;\ \frac{Sx}{Sb}=3.357143;\ \frac{Sx}{Sc}=2.238095$$

$$W=10.599295;\ W'=0.230365;\ \chi^2=10.829660$$

In such problems as those illustrated in which the main effects differ materially, the heterogeneity χ^2 is preferred to the interaction χ^2 obtained by partitioning the total χ^2 into its components. However, in many problems it is not necessary to calculate the heterogeneity χ^2, which involves much more work.

EXPERIMENTAL RESULTS

It can be seen from table 1, without detailed statistical analysis, that meiosis is essentially normal as regards synapsis. This fact is readily appreciated when it is recalled that the figures in the individual categories represent the number of cells among 100 examined that showed at least 1 univalent chromosome. Hence, asynapsis is not frequent enough to interfere materially with the obtaining of double crosses and advanced and backcross populations. It follows, then, that asynapsis is not a factor in breeding new varieties of strawberries by the hybridization method in which × *Fragaria ananassa* and *F. ovalis* are used as parents.

The occurrence of associations of more than two chromosomes to form multivalents during meiosis was so infrequent as not to merit tabulation. It may be concluded, therefore, that this phenomenon also presents no problem in breeding strawberries by the hybridization method in which × *Fragaria ananassa* and *F. ovalis* are used as the parents.

The third major problem is that of determining the type of conjugation occurring during meiosis of the F_1 hybrids. If autosyndesis is taking place during meiosis of the F_1 hybrids between × *Fragaria ananassa* and *F. ovalis*, then the × *F. ananassa* chromosomes are pairing with × *F. ananassa* chromosomes and the *F. ovalis* chromosomes with *F. ovalis* chromosomes. By using the previously given symbols for the chromosome complements of × *F. ananassa* and *F. ovalis*, autosyndesis in the F_1 hybrids may be illustrated as follows:

× *F. ananassa:*
Acv$_1$; *Acv*$_2$; *Acv*$_3$; *Acv*$_4$
Acv$_1$; *Acv*$_2$; *Acv*$_3$; *Acv*$_4$
F. ovalis:
Ao$_1$; *Ao*$_2$; *Ao*$_3$; *Ao*$_4$
Ao$_1$; *Ao*$_2$; *Ao*$_3$; *Ao*$_4$
F_1 hybrid:
Acv$_1$; *Acv*$_2$; *Ao*$_1$; *Ao*$_2$
Acv$_3$; *Acv*$_4$; *Ao*$_3$; *Ao*$_4$

From the above it is clear that, if autosyndesis is occurring, all of the F_2 populations would be composed of four complete sets of × *F. ananassa* chromosomes and four complete sets of *F. ovalis* chromosomes. Hence, if × *F. ananassa* chromosomes do not conjugate with *F. ovalis* chromosomes, there is no opportunity for segregation of the genes differentiating the interspecific characters, that is, those genes differentiating the characters by which the species differ.

Similarly, allosyndesis in an F_1 hybrid may be illustrated as follows:

Acv$_1$; *Acv*$_2$;*Acv*$_3$; *Acv*$_4$
Ao$_1$; *Ao*$_2$; *Ao*$_3$; *Ao*$_4$

From this illustration it can be seen that the maximum opportunity for segregation of the genes differentiating the interspecific characters would occur during meiosis.

One form of a combination of the two types of conjugation in an F_1 hybrid may be illustrated as follows:

Acv$_1$; *Ao*$_1$; *Acv*$_3$; *Acv*$_4$
Acv$_2$; *Ao*$_2$; *Ao*$_3$; *Ao*$_4$

From this illustration it can be seen that in some cases × *Fragaria ananassa* chromosomes are paired with × *F. ananassa* chromosomes; in other cases they are paired with *F. ovalis* chromosomes. It follows that in some instances *F. ovalis* chromosomes are paired with *F. ovalis* chromosomes; in others they are paired with × *F. ananassa* chromosomes. Hence, the opportunity for segregation of the genes differentiating the interspecific characters is intermediate between those of autosyndesis and allosyndesis.

From these considerations it is evident that the type of pairing of the chromosomes (autosyndesis, allosyndesis, or a combination of the two) materially influences the segregation of the genes that differentiate the interspecific characters. The commonest method of chromosome pairing of polyploid organisms is allosyndesis. With this fact in mind, Wright (*28, p. 45*) has shown that—

> a random-bred stock derived from n inbred families will have $\frac{1}{n}$th less superiority over its inbred ancestry than the first cross or a random-bred stock from which the inbred families might have been derived without selection.

Kiesselbach (*12*), working with plants, reached a similar conclusion.

Wright has developed formulas for use when the effects of the genes differentiating the characters under consideration are geometrically cumulative. For these formulas and their application, the reader is referred to Powers (*22*) and Powers and Lyon (*23*). These formulas as well as those based on the assumption that the effects of the genes are arithmetically cumulative assume that allosyndesis is occurring during meiosis of the F_1 hybrid. Thus it is clear that, if the means of the interspecific characters can be predicted by the use of Wright's formulas, allosyndesis must be occurring during meiosis of the microsporocytes and the megasporocytes at least as regards the chromosomes containing the genes which differentiate the characters under consideration. On the other hand, if autosyndesis is the rule, segregation of the genes differentiating the interspecific characters would be materially limited and the means of the characters for the F_2 populations should closely approximate the means of the same characters for the F_1 populations.

In making these tests the studies will be more conclusive if the magnitude of the effects of the genes differentiating the two species is quite large as regards the character under consideration and if the characters are based on absolute rather than observational measurements. The characters which meet these specifications are plant height measured in centimeters, number of days from May 1 to first bloom, and number of days from first bloom to first fruit ripe. Although based only on observational grades, the degree of winter injury was very marked and, therefore, this character also was included in the study. The degree of winter injury increases from grade 1 to grade 5.

The data are presented in table 3. The theoretical means listed are those calculated on the assumption that the effects of the genes differentiating the respective characters are arithmetically cumulative. The fit between the theoretical means calculated on the assumption that the effects of the genes are geometrically cumulative and the obtained means (with the exception of the means for grades of winter injury) was definitely poorer than the fit between the means calculated on the assumption that the effects of the genes are arithmetically cumulative and the obtained means. Since such is the case, there would not be much point in listing the theoretical geometric means. In respect to winter injury the geometric mean for the backcross to Fairfax fitted the obtained mean better than did the arithmetic mean, but for the F_2 population the reverse was true.

TABLE 3.—*The obtained and theoretical arithmetic means and their standard errors for different characters of the cross Fairfax × Fragaria ovalis (36979)*

Variate	Winter injury		Plant height		Period from May 1 to first bloom		Period from first bloom to first fruit ripe	
	Obtained	Theoretical	Obtained	Theoretical	Obtained	Theoretical	Obtained	Theoretical
	Grade	*Grade*	*Centimeters*	*Centimeters*	*Days*	*Days*	*Days*	*Days*
Fragaria ovalis (36979):								
Asexual	1.00±0.170		11.3±0.597		14.2±0.696		46.0±0.943	
Selfed (S_1)	1.06± .124		8.8± .554		14.5± .477		49.1± .605	
Hybrid populations:								
Backcross [(Fairfax×36979)×36979]	1.07± .141	1.16±0.112	16.3± .633	14.5±0.448	14.3± .517	15.3±0.371	44.6± .702	43.8±0.510
F_1 (Fairfax×36979)	1.32± .146		17.7± .668		16.3± .260		40.8± .389	
F_2 (Fairfax×36979)	2.03± .107	2.19± .111	13.1± .345	14.1± .475	22.3± .472	19.7± .870	40.5± .330	40.2± .591
Backcross [Fairfax×(Fairfax×36979)]	2.79± .132	3.21± .110	14.2± .395	13.7± .501	25.2± .610	24.1±1.173	36.3± .515	36.9± .662
×*F. ananassa* (Fairfax):								
Selfed (S_1)	4.65± .169		9.6± .748		31.8±2.332		33.0±1.265	
Asexual	5.10± .165							

The means for winter injury and for days from May 1 to first bloom ranged from that of *Fragaria ovalis* asexually propagated to that of Fairfax asexually propagated or self-pollinated; for days from first bloom to first fruit ripe the means ranged from that of the progeny of Fairfax self-pollinated to that of the progeny of *F. ovalis* self-pollinated. In plant height, for which the F_1 hybrid shows decided heterosis, the means ranged from that of the progeny obtained by self-pollinating *F. ovalis* to that of the F_1 hybrid. These data are in accord with what would be expected if allosyndesis was occurring during meiosis of the F_1 hybrid. It will be recalled that in case autosyndesis was the common mode of behavior the mean of the F_2 population would be expected to be similar in magnitude to that of the F_1 hybrid. As may be seen from the data in table 3, such definitely was not the case as regards winter injury, plant height, and days from May 1 to first bloom. As regards days from first bloom to first fruit ripe, a comparison of the means for the F_1 hybrid and the F_2 population does not indicate whether allosyndesis or autosyndesis is the rule. The reason for this is that the theoretical arithmetic mean based on allosyndesis is so close to that of the F_1 hybrid that any differences noted can logically be attributed to chance deviations. Probably the most convincing evidence that allosyndesis rather than autosyndesis or a combination of allosyndesis and autosyndesis is the rule during meiosis of the F_1 hybrid is that in 10 cases out of a possible 12 (see Tippett *27, p. 54*) the differences between the obtained and theoretical means can logically be attributed to chance deviations.

In summing up it may be said that the evidence, which is rather conclusive, is preponderantly in favor of allosyndesis as the type of conjugation that occurs during meiosis of the F_1 hybrids, and it appears certain that any deviation from allosyndesis is not of sufficient importance to interfere materially with obtaining the objectives of a breeding program in which $\times$ *Fragaria ananassa* (variety Fairfax) and *F. ovalis* (collection 36979) are the parents.

From the foregoing it can be seen that the major problems which the experiment was designed to answer have been solved. However, the data furnish additional information which, though of only minor importance to the breeding program at Cheyenne, may be of interest to other investigators working with the cytogenetics of *Fragaria*.

The χ^2 values for testing goodness of fit between the theoretical based on the supposition that there are no differences between species, between strains, or between phases, together with those χ^2 values for testing whether the interactions are statistically significant, are given in table 4. From these data it seems probable that differences exist between species, between strains, and between phases. However, the differences between strains are not so well established statistically as the differences between species or between phases. The only interaction approaching statistical significance is that between species and strains. The heterogeneity χ^2 for this interaction is 10.830, which is highly significant.

The meaning of these differences can best be found by examining the data in table 1. The differences between species there shown were due to the fact that failure of chromosome pairing was somewhat greater in the native Rocky Mountain strawberry than in the cultivated strawberry. The possible differences between strains were due to the fact that the failure of chromosome pairing was at least

partially dominant in the F_1 hybrid of Fairfax × 36979 and at least partially recessive in the F_1 hybrids of Dorsett × 37501 and Gem × 361477. The differences between phases were due to the fact that the number of cells showing irregularities was greater for the metaphase of the first division than for the telophase of that division and either stage of the second division. The explanation for this may be the same as that found by Powers (*21*) in similar studies with *Triticum aestivum*.

TABLE 4.—χ^2 *values for the different components*

Source of variation	Degrees of freedom	χ^2
Main effects:		
Species	2	12.868
Strains	2	5.855
Phases	3	7.909
Interactions:		
Species × strains	4	8.826
Species × phases	6	3.037
Strains × phases	6	4.020
Species × strains × phases	12	8.826
Total	35	51.341

Environment is a factor that must be considered in evaluating the importance of the frequency of failure of chromosome pairing to a crop-improvement program. The investigations of Stow (*26*), Heilborn (*9*), Randolph (*24*), and Myers and Powers (*20*) definitely show that the differences in environment encountered under field conditions have diverse effects on synapsis. So it must be concluded that, even though asynapsis influences the breeding program very little under the environmental conditions existing at Cheyenne, Wyo., it may be of major importance under the environmental conditions of other locations. For this reason, selections made at Cheyenne from material resulting from crossing ×*Fragaria ananassa* and *F. ovalis* may fail when grown in other localities.

SUMMARY

Cytological data, taken from three cultivated varieties of strawberry (×*Fragaria ananassa*), three collections of the native Rocky Mountain strawberry (*F. ovalis*), and three F_1 interspecific hybrids involving these collections and varieties, are reported.

New formulas for χ^2 are given, and their application is illustrated. These formulas reduce the labor involved in calculating χ^2 when the number of categories of the table used in the calculations is large.

The breeding data show rather conclusively that meiotic instability is at most a minor problem under the environmental conditions prevailing at Cheyenne, Wyo.

The segregation of the genes differentiating certain characters, as indicated by the means of these characters for different populations, furnishes rather convincing evidence that allosyndesis is the rule during meiosis of the F_1 hybrids.

So far as meiotic irregularities and the method of pairing of the chromosomes are concerned, there does not seem to be any reason why the economically important characters of ×*Fragaria ananassa*

and *F. ovalis* cannot be recombined into a single variety adapted to production under the environmental conditions encountered at Cheyenne, Wyo.

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